Energetics of the Ventilatory Piston Pump of the Lugworm, a Deposit-feeding Polychaete Living in a Burrow

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Abstract. The aim of this study was to tentatively estimate the energy cost of breathing in the lugworm, *Arenicola marina* (L.), a gallery-dwelling, piston-pump breather that moves water in a tail-to-head direction. Each tested lugworm was placed in a horizontal glass tube. The caudal end of the tube was connected to a well-aerated seawater reservoir at 20°C, and the cephalic end attached to a drop meter through a tube resistance. At the exit of the cephalic chamber the O_2 tension was recorded via an *in situ* O_2 electrode, and the hydrostatic pressure of the exhaled water was also recorded. Water flow rate, total O_2 uptake rate $\dot{M}_{O_2}^{TOT}$, O_2 extraction coefficient, and the mechanical power necessary to pump water through the resistive anterior exit of the apparatus ($\dot{W}_{MEC}$), were computed. The basal metabolic rate of each animal ($\dot{M}_{O_2}^{CONF}$) was separately estimated by the confinement method. $\dot{M}_{O_2}^{CONF}$ subtracted from $\dot{M}_{O_2}^{TOT}$ approximates $\dot{M}_{O_2}^{CB}$, the O_2 uptake rate necessary to activate the piston-pump breathing mechanism and to ensure the corresponding mechanical work rate, $\dot{W}_{MEC}$.

The results show that the energy cost of breathing, $\dot{M}_{O_2}^{CB}$, of the piston-pump-breathing *Arenicola* is very high, with mean values approximating 47% of the $\dot{M}_{O_2}^{TOT}$ value; that the mechanical power we measured, $\dot{W}_{MEC}$, is very low; and that the mechanical-to-metabolic efficiency, the ratio $\dot{W}_{MEC}/\dot{M}_{O_2}^{CB}$, does not exceed 1%. These observations are compared to those obtained in other piston-pump breathers, such as *Chaetopterus variopedatus* and *Urechis* *caupo*, and in ciliary filter feeders including polychaetes, bivalves, and ascidians.

Introduction

Most aquatic macrofauna burrowing in soft substrates maintain direct contact with the water covering the sediments via tube or gallery systems through which water is pumped. The animal thus meets its respiratory needs and, in the case of a filter feeder, eventually obtains the particulate matter on which it feeds (Newell, 1979). The lugworm, *Arenicola marina*, is a deposit feeder (Jacobsen, 1967). It lives in a permanent L-shaped gallery deeply dug in intertidal sands and communicating with the water column through a single posterior (caudal) opening. During high tide, the lugworm actively pumps water that flows over the animal's body and then percolates through the sand blocking the blind head-end of the burrow. In this piston-type pumping mechanism, the burrow is rhythmically sealed by tail-to-head peristaltic movements of the body wall which force the inspired seawater forward (Wells, 1966; Foster-Smith, 1978).

A positive displacement pump such as a piston pump is the only possible biological pump that can generate the high hydrostatic pressure needed to force water through a tube system with a high flow resistance. This pumping mechanism, however, can produce only moderate water flow rates, and it is considered to be energetically expensive (Walshe-Maetz, 1953; Mangum, 1976). Some indirect evidence suggests that this statement could be valid in the case of the lugworm: (1) despite the efficiency of its respiratory exchanger, which can extract up to 90% of the oxygen in normoxic water, the lugworm does not regulate its O_2 uptake rate below an O_2 partial pressure of 15 kPa in the inspired water; (2) hypoxia below 5.3 kPa is clearly

a signal to stop ventilating; (3) from data obtained in previous experiments under normoxic conditions, it can be calculated that the O_2 uptake necessary to cover the ventilatory work—that is, the energy cost of breathing, $\dot{M}_{O_2}^{CB}$—corresponds to about 40% of the total O_2 uptake (Toulmond, 1975, 1986; Toulmond and Tchernigovtzeff, 1984). The aim of this work is to obtain direct evidence concerning the characteristics and the energetics of the ventilatory piston pump of a deposit feeder, the lugworm, and to compare it with the piston pump of filter feeders such as *Chaetopterus variopedatus* (Brown, 1975; Riisgård, 1989) and *Urechis caupo* (Chapman, 1968; Pritchard and White, 1981).

Principles

The total O_2 uptake from the environment, $\dot{M}_{O_2}^{TOT}$, of a lugworm ventilating in its gallery during a certain period of time is the product of the water flow times the difference of O_2 concentration between inspired and expired water, itself resulting from the multiplication of the inspired-to-expired P_{O_2} difference by the O_2 solubility. $\dot{M}_{O_2}^{TOT}$ is the sum of three terms:

$$M_{O_2}^{TOT} = M_{O_2}^{CONF} + M_{O_2}^{CB} + \Delta M_{O_2}^{STO} \qquad (1)$$

$M_{O_2}^{CONF}$ is the O_2 uptake of a lugworm doing no ventilatory work and is considered here as a measure of the basal metabolism of the animal. If the O_2 stores are kept constant, $M_{O_2}^{CONF}$ can be evaluated in a lugworm confined motion-free in a large closed flask, taking into account the flask volume and the initial and final ambient P_{O_2} values, the final P_{O_2} being above the critical point, P_C, the O_2 pressure below which the O_2 stores are used (Toulmond, 1975).

$M_{O_2}^{CB}$ is the O_2 uptake necessary to cover the ventilatory work, that is, the energy cost of breathing, CB.

$\Delta M_{O_2}^{STO}$ is the eventual change of O_2 stores. If the O_2 stores remain constant, $\Delta M_{O_2}^{STO}$ is null, and equation (1) is simplified to

$$M_{O_2}^{TOT} = M_{O_2}^{CONF} + M_{O_2}^{CB} \qquad (2)$$

In this case, where the O_2 uptake from the environment is entirely used to cover the aerobic cellular metabolism, $M_{O_2}^{TOT}$ is the metabolic O_2 consumption, $M_{O_2}^{MET}$:

$$M_{O_2}^{MET} = M_{O_2}^{TOT} = M_{O_2}^{CONF} + M_{O_2}^{CB} \qquad (2a)$$

If the O_2 stores change, $\Delta M_{O_2}^{STO}$ is different from zero. The term can be either negative (when the O_2 stores decrease) or positive (when the O_2 stores increase). Then equation (2a) becomes

$$M_{O_2}^{MET} = M_{O_2}^{TOT} \pm \Delta M_{O_2}^{STO} = M_{O_2}^{CONF} + M_{O_2}^{CB} \qquad (3)$$

In practice, we measured the total O_2 uptake from the environment, $M_{O_2}^{TOT}$, of a lugworm ventilating in an ar-

tificial gallery through a given resistance, and the O_2 uptake of the same animal confined as described above, $M_{O_2}^{CONF}$. Owing to the special, periodical ventilation of the lugworm (see Discussion; Validity of the model), one has to distinguish two types of values for $M_{O_2}^{TOT}$.

The symbol $lgM_{O_2}^{TOT}$ corresponds to mean values obtained through "long duration" (91 to 178 min) measurement periods. In this first case, the O_2 stores can be considered as identical at the beginning and at the end of the measurement period, equation (2) applies, and the energy cost of breathing, $M_{O_2}^{CB}$, can be estimated.

The symbol $shM_{O_2}^{TOT}$ corresponds to values obtained through "short duration" (6 min) measurement runs. In this second case, the O_2 stores can be different at the beginning and at the end of a given measurement run, and equation (3) applies. Because the value of $\Delta M_{O_2}^{STO}$ is unknown, $M_{O_2}^{CB}$ cannot be estimated (see Discussion).

Materials and Methods

Experiments were carried out in Roscoff, Nord-Finistère, France, in August 1988 and in May–August 1989. Medium-sized lugworms, wet mass 15 to 20 g, were collected on the nearby Penpoull beach, brought back to the laboratory, and kept unfed overnight in local running seawater (temperature 14 to 16°C) to free the gut of sand.

### *Measurement of total O_2 uptake rate, $\dot{M}_{O_2}^{TOT}$, in an artificial gallery*

The artificial gallery consisted of a straight glass tube 30 cm long, i.d. 1 cm, horizontally immersed in a 40-l holding tank (Fig. 1).

The rear (caudal) end of the tube was connected by glass tubing to an open, constant level, 1-l bottle containing seawater bubbled with air. To attenuate the transmission of vibrations, this tonometer was kept in a separate tank. Both tanks were supplied with decanted flowing natural seawater maintained at a thermostat setting of 20°C.

At the anterior (cephalic) end of the tube were serially fitted (1) a small acrylic chamber containing a Radiometer E5046 O_2 electrode, immediately followed by a T-connection to a P23BB Statham pressure gauge; (2) two different parallel lengths of tubing, provided with stopcocks, which gave two different resistance values, R1 or R2, at the exit; (3) a photocell drop counter.

The water level of the apparatus was continuously maintained the same at both ends of the system. Under these conditions, in accordance with Poiseuille's law, the lugworm ventilating from tail to head had to create a certain hydraulic pressure difference to overcome the terminal resistance of the system.

The three measured variables were the O_2 pressure in the expired water ($P_{E_{O_2}}$), the hydrostatic pressure difference before the exit resistance (ΔP_{HYD}), and the water flow (V_w).
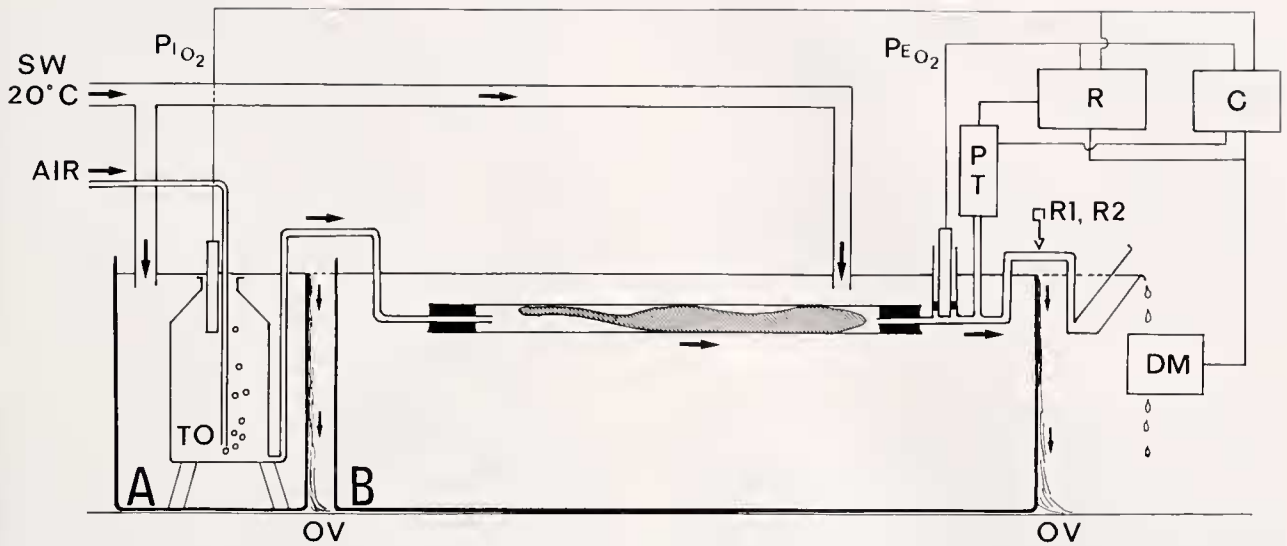
Figure 1. Apparatus. The glass tube containing the lugworm was placed in a thermostatted seawater bath. The rear (caudal) part of the tube was connected through very low-resistance glass tubing to a constant level tonometer (TO) equipped with an O_2 electrode measuring the O_2 partial pressure in the inspired water (PI_{O_2}). At the anterior (cephalic) end of the tube were serially fitted (1) a small acrylic chamber containing an O_2 electrode measuring the O_2 partial pressure in the expired water (PE_{O_2}), immediately followed by a T-connection to a pressure transducer (PT); (2) two different tubing lengths corresponding to two different exit resistances, R1 and R2; and (3) a photocell drop meter (DM). A and B: separated water baths; OV: overflow; R: potentiometric recorder; C: microcomputer; Arrows: direction of air or water circulation.

Twelve hours after collection, a lugworm (mean wet mass: 18.5 ± 1.7 g, $N = 10$) was placed unrestrained in the artificial gallery; measurements were started about 1 h later. Each experiment was carried out on a different animal and was divided into three periods lasting between 90 and 180 min each and corresponding to a different exit resistance. One day the sequence was R1, R2, R1 and the next day R2, R1, R2, to cancel the possible influence of fatigue. During each period, PE_{O_2}, $\Delta PHYD$ and $\dot{V}w$ were continuously recorded graphically by a potentiometric recorder. In parallel, when the lugworm ventilated in a regular and continuous way, PE_{O_2} and $\Delta PHYD$ were recorded on tape by a Hewlett-Packard HP85B microcomputer for separate runs each lasting 6 min. For each period, 12 to 15 runs were recorded.

During each run, the corresponding total volume of ventilated water, Vw, was collected and measured to the nearest 0.1 ml with a measuring cylinder. This value; the calibration coefficients for the O_2 electrode and the pressure gauge; the O_2 solubility coefficient at 20°C, $\alpha = 0.0000116$ μmol/(ml·Pa); and the O_2 pressure in the ingoing seawater, PI_{O_2}, were introduced into the computer, which calculated 6-min mean values of (1) the water flow rate, $\dot{V}w$; (2) the O_2 extraction coefficient, $EW_{O_2} = (PI_{O_2} - PE_{O_2})/PI_{O_2}$; (3) the short duration total O_2 uptake rate, $sh\dot{M}_{O_2}^{TOT} = \dot{V}w (CI_{O_2} - CE_{O_2})$; (4) the specific ventilatory rate, $\dot{V}w/sh\dot{M}_{O_2}^{TOT}$; (5) the hydrostatic pressure difference, $\Delta PHYD$; (6) the hydraulic resistance, $R = \Delta PHYD/\dot{V}w$;

and (7) the mechanical power, $\dot{W}_{MEC} = \Delta PHYD \times \dot{V}w$, developed to push water from the cephalic end of the gallery to the final exit of the circuit. All values were expressed in SI units. For O_2 consumption, we took the value of 450 J/mmol O_2 as the SI unit for the oxy-energetic equivalent (see Dejours, 1981).

At the end of an experiment, the three periods were separately analyzed using the graphical record of PE_{O_2}, $\Delta PHYD$, and the drop counter signal. The total duration of each period was measured, including the ventilatory arrests not lasting more than 20 min (beyond this duration, the O_2 stores are exhausted and the metabolism turns anaerobic), as well as the corresponding long duration mean total O_2 uptake, $1g\dot{M}_{O_2}^{TOT}$, evaluated using the $sh\dot{M}_{O_2}^{TOT}$ previously calculated for each 6-min run. The O_2 uptake between two runs was obtained by interpolation.

Measurement of the basal metabolism rate, $\dot{M}_{O_2}^{CONF}$, by confinement

After the total O_2 uptake in the artificial gallery had been measured, the worm was transferred to a 575-ml opaque vessel wrapped in an aluminum sheet and filled with normoxic water. The vessel was thereafter closed hermetically and placed at 20°C. The confinement, which lasted about 90 min, was discontinued when P_{O_2} was around the critical O_2 pressure, roughly 15 kPa. Knowing

the volumes of the bottle and of the animal, the initial and final P_{O_2} of the water, and the confinement duration, we calculated the basal metabolic rate, $\dot{M}_{O_2}^{CONF}$.

Determination of the cost of breathing, $\dot{M}_{O_2}^{CB}$

Assuming that the O_2 stores were identical at the beginning and end of each long duration measurement period, the mean rate of energy cost of breathing was then calculated as $\dot{M}_{O_2}^{CB} = 1g\dot{M}_{O_2}^{TOT} - \dot{M}_{O_2}^{CONF}$.

Results

We conducted 22 experiments on 22 different lugworms. All animals responded similarly. The results reported here concern the last 10 experiments, the only ones to be completely analyzed. Results for *Arenicola* #21 were selected to illustrate this analysis because they were among the most representative of this very coherent set of experiments. Values are means ± 1 SD. Differences between means were evaluated using Student's t test with $P = 0.05$ as the fiducial limit of significance.

Figures 2 to 6 report results for *Arenicola* #21; a value of $\dot{M}_{O_2}^{CONF} = 3000$ μW was measured for this animal during an 89-min confinement period. Each point corresponds to one 6-min run. The ventilatory flow rate, $\dot{V}w$ (Fig. 2),
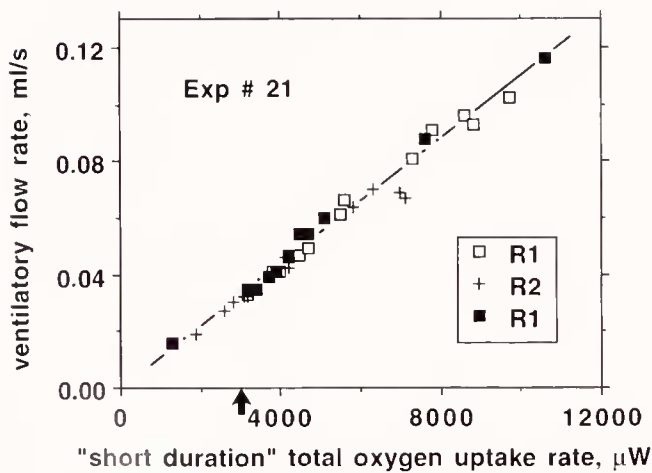

Figure 2. *Arenicola* #21 (wet mass: 17.2 g). Ventilatory flow rate, $\dot{V}w$, as a function of the "short duration" total O_2 uptake rate, sh$\dot{M}_{O_2}^{TOT}$ ($y = 0.000011$ $x + 0.0009$; $r = 0.990$). Note that the slope of the regression line is the M_{O_2}-specific ventilation, namely 0.000011 ml/μJ (about 5 l/mmol O_2), a relatively low value for a water breather (Dejours, 1981), well in line with the high extraction coefficient in *Arenicola*. Open and closed squares correspond to breathing against a low resistance, R1, during the first and third period of the experiment; crosses concern breathing against the higher resistance R2 during the second period of the experiment (see text, Materials and Methods). The arrow on the abcissa corresponds to the value of the basal metabolism of lugworm #21, as measured by confinement. $\dot{M}_{O_2}^{CONF} = 3000$ μW. Mean value of $\dot{M}_{O_2}^{CB} = 1150$ μW. We took the value of 450 J for 1 mmol O_2 as the SI unit for the oxy-energetic equivalent (Dejours, 1981).
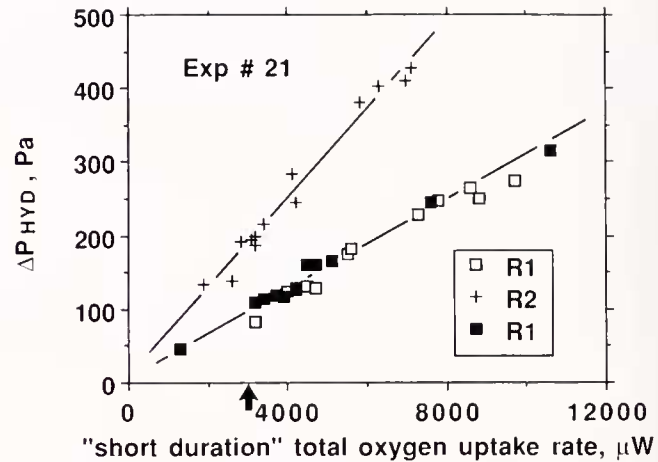

Figure 3. *Arenicola* #21. ΔPHYD, difference of hydrostatic pressure between the anterior chamber and atmosphere, as a function of the "short duration" total O_2 uptake rate, sh$\dot{M}_{O_2}^{TOT}$. R1 and R2 correspond to the low and high exit resistances opposed to exhaled water. Symbols as in Figure 2. Equation corresponding to R1: $y = 0.29$ $x + 10.2$ ($r = 0.988$), and to R2: $y = 0.6$ $x + 8.9$ ($r = 0.987$).

and the hydrostatic pressure difference, ΔPHYD (Fig. 3), were directly proportional to the short duration oxygen uptake rate, sh$\dot{M}_{O_2}^{TOT}$. These figures also show that there was no significant difference between the first and the subsequent periods, indicating that the animal did not tire. Figure 2 shows that the resistance (R1 or R2) apparently did not influence the ventilatory flow rate, whereas Figure 3 shows, as expected, that the hydrostatic pressure difference was higher in the experiments with greater expiratory load (R2 $\sim$ 2R1).

Figure 4 describes the variations, as a function of sh$\dot{M}_{O_2}^{TOT}$, of the mechanical power, $\dot{W}_{MEC}$, developed to overcome the resistive respiratory loading, R1 or R2. Calculation of the corresponding log-log regressions shows that $\dot{W}_{MEC}$ varies as a quadratic function of sh$\dot{M}_{O_2}^{TOT}$, a necessary consequence of the linearity observed in Figures 2 and 3.

Finally, Figure 5 shows the variations of the difference of pressure between the anterior chamber and the ambient air, ΔPHYD, as a function of the ventilatory flow rate, $\dot{V}w$, through the exit resistances R1 and R2 whose mean values, respectively 2600 and 5900 Pa·s/ml, are given by the slope of the regression lines (see legend of Fig. 5). This figure also shows that, as needed by Poiseuille's equation, the ventilatory flow rate is directly and linearly proportional to ΔPHYD, and inversely proportional to the resistance of the setup. This fine tuning between the theory and the data can be considered as a positive argument for the validity of our measurement methods and the conditions in which the lugworm had to ventilate.

In some 6-min runs, we could estimate the pumping frequency of the piston pump's periodic activity by mea-
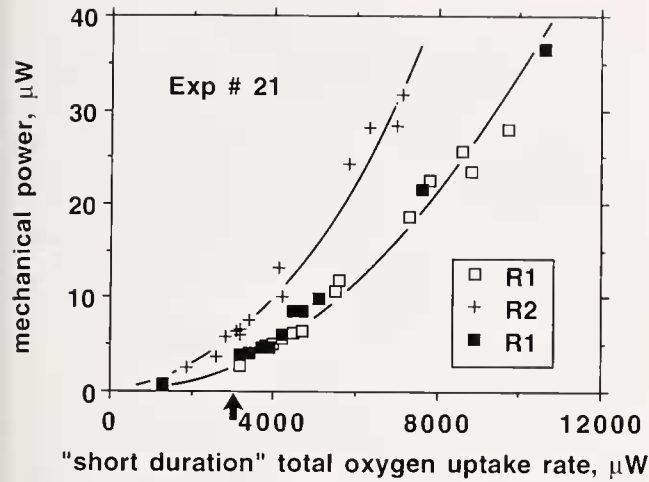
Figure 4. *Arenicola* #21. Mechanical power, $\dot{W}_{MEC}$, necessary to obtain the flow of water through either the low resistance R1 or the higher resistance R2, as a function of the total energy expenditure estimated as the "short duration" total O_2 uptake, $sh\dot{M}_{O_2}^{TOT}$. The drawn curves were fitted by eye. Symbols as in Figure 2. Equation corresponding to R1: $y = x^{1.91}/(7.9 \cdot 10^6)$ ($r = 0.991$) and to R2: $y = x^{1.99}/(6.3 \cdot 10^6)$ ($r = 0.991$) (see text).
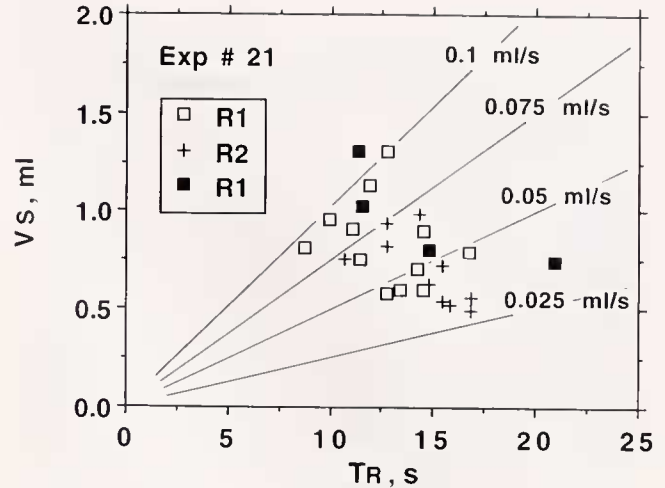

Figure 6. *Arenicola* #21. Water stroke volume, Vs, *versus* the duration of successive ventilatory cycles, TR, with the animal breathing through a low resistance, R1, or a high resistance, R2. The oblique lines correspond to various iso-ventilatory flow rates, in milliliters per second. Symbols as in Figure 2. Mean values for R1 ($N = 16$): Vs $= 0.87 \pm 0.23$ ml; TR $= 13.1 \pm 2.9$ s; $\dot{V}w = $ Vs/TR $= 0.069 \pm 0.026$ ml/s. Mean values for R2 ($N = 10$): Vs $= 0.70 \pm 0.18$ ml; TR $= 14.5 \pm 2.0$ s; $\dot{V}w = $ Vs/TR $= 0.049 \pm 0.017$ ml/s. Only the $\dot{V}w$ values are significantly different.

suring the duration of each respiratory period, TR, and calculating the stroke volume of the pump, Vs, according to the equation Vs $= \dot{V}w \times$ TR. Figure 6 shows that the breathing pattern was similar whether the animal was breathing against a low or high resistance. However, the ventilatory flow rate under high resistance was significantly lower than under low resistance, with a small, nonsignif-

icant decrease of the stroke volume and a small, nonsignificant increase of the ventilatory period (see legend of Fig. 6 for statistics).
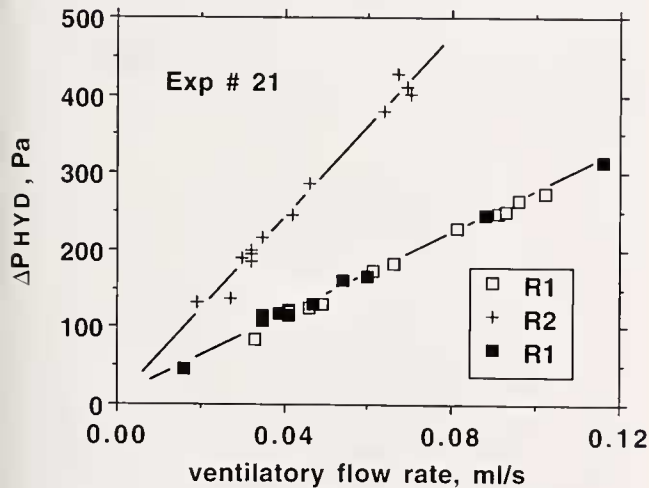

Figure 5. *Arenicola* #21. ΔPHYD, difference of pressure between the anterior chamber and atmosphere, as a function of $\dot{V}w$, the ventilatory flow rate through low and high resistances, R1 and R2. Values of ΔPHYD and $\dot{V}w$ from Figures 2 and 3. The slopes of the regression lines correspond to the mean values of R1 and R2, about 2600 and 5900 Pa·s/ml. Symbols as in Fig. 2. Equation corresponding to R1: $y = 2635 x + 10$ ($r = 0.996$), and to R2: $y = 5917 x + 5$ ($r = 0.991$).
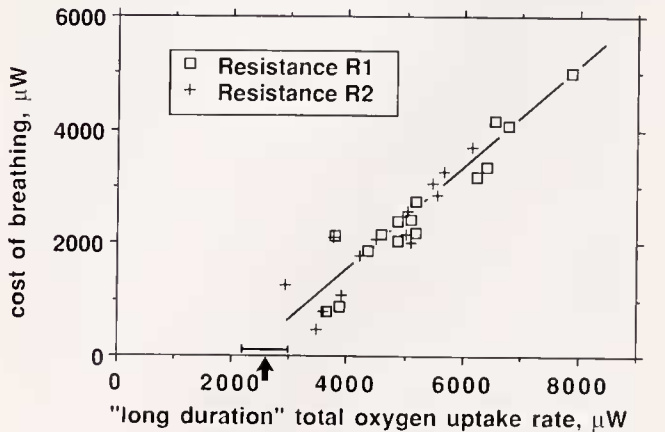

Figure 7. Energy cost of breathing, $\dot{M}_{O_2}^{CB}$, as a function of the "long duration" total O_2 uptake rate, $lg\dot{M}_{O_2}^{TOT}$, of *Arenicola* breathing through a resistance R1 (*ca* 2600 Pa·s/ml) or R2 (*ca* 5900 Pa·s/ml). Values for 10 experiments of three periods, each animal breathing successively through resistances R1, R2, R1 or R2, R1, R2. The arrow on the abcissa at 2600 ± 400 μW ($N = 10$) corresponds to the measure of the basal metabolism of the lugworm, *i.e.*, the mean O_2 uptake rate of an animal doing no ventilatory work, as measured by confinement, $\dot{M}_{O_2}^{CONF}$. The O_2 uptake rate above $\dot{M}_{O_2}^{CONF}$ is considered as the energy cost of breathing. The slope of the regression line ($y = 0.89 x - 2024$; $N = 30$; $r = 0.838$) is not significantly different from the theoretical value of 1 (see equation 2).

Figure 7 summarizes for the 10 experiments the relationship between the energy cost of breathing, $\dot{M}_{O_2}^{CB}$, and the long duration total oxygen uptake rate, $1g\dot{M}_{O_2}^{TOT}$. Each value corresponds to one period of 126 ± 23 min ($N = 30$) and to either the R1 or R2 value of the resistance at the anterior exit. The $\dot{M}_{O_2}^{CB}/1g\dot{M}_{O_2}^{TOT}$ ratio varied between 0.14 and 0.64, with a mean value of 0.47. The regression line, corresponding to the mean variations of $\dot{M}_{O_2}^{CB}$ over $1g\dot{M}_{O_2}^{TOT}$, intersects the x-axis within the variation interval of the mean basal metabolism measured by the confinement method, $\dot{M}_{O_2}^{CONF} = 2600 \pm 400$ μW ($N = 10$). It is clear that there was no systematic difference between the R1 and R2 periods and that the energy cost of breathing increased linearly with the rise of $1g\dot{M}_{O_2}^{TOT}$.

Discussion

Validity of the model, hypotheses, and methods

Equation (2) is valid only in steady state conditions, that is, when the term $\Delta\dot{M}_{O_2}^{STO}$ is null. In the lugworm, the ventilation is periodic, with ventilatory bouts lasting 10 to 15 min, separated by pauses of a few minutes during which the O_2 stores can be partially depleted but then are quickly restored during the following ventilatory phase. Consequently, in the lugworm, equation (2) is valid only in the long term, in experiments that last a few hours and allow us to consider that any difference in the size of the O_2 stores at the beginning and at the end of an experiment is negligible relative to the overall O_2 uptake during the experiment. This is the case when we consider R1 and R2 periods lasting an average of 126 ± 23 min (Fig. 7).

Conversely, when we analyze separately each of the short 6-min runs in a given period (for example, *Arenicola* #21, Figs. 2 to 6), it is clear that equation (2) does not apply to all runs. This is demonstrated by Figs. 2 to 4, in which the lowest values of ventilatory flow rate, of ΔP_{HYD}, and of mechanical power correspond to values of $sh\dot{M}_{O_2}^{TOT}$ that are lower or equal to $\dot{M}_{O_2}^{CONF}$, and consequently correspond to impossible negative or null values of this variable. Obviously, the term $\Delta\dot{M}_{O_2}^{STO}$ was not identical at the beginning and at the end of the corresponding runs: the lowest $sh\dot{M}_{O_2}^{TOT}$ values correspond to a depletion of the O_2 stores, whereas the highest $sh\dot{M}_{O_2}^{TOT}$ values correspond to their restoration. It is important to note that when the animal is in complete apnea, then $\dot{V}w = 0$, implying $sh\dot{M}_{O_2}^{TOT} = 0$, and the aerobic metabolism totally depends on the O_2 stores. In all cases, however, if our evaluations of $\dot{V}w$, ΔP_{HYD}, and $sh\dot{M}_{O_2}^{TOT}$ are correct, then their analysis is pertinent, giving information on the ventilatory pump and its energetics.

Does $\dot{M}_{O_2}^{CONF}$ correctly estimate the basal O_2 uptake rate? A lugworm in a confinement vessel, deprived of normal contacts with its gallery walls, is never perfectly still. Actually, the tail-to-head peristaltic movements of the body wall are more or less preserved, but they do not produce a true external ventilatory current of seawater. Then the oxygen consumption corresponding to the mechanical work achieved during the confinement can be considered as negligible compared with that occurring in an animal ventilating through an exit resistance in its artificial gallery. However, it is quite certain that $\dot{M}_{O_2}^{CONF}$ slightly overestimates the basal metabolism, leading to the conclusion that $\dot{M}_{O_2}^{CB}$ is slightly underestimated.

Cost of breathing and energetics and respiratory strategy in the lugworm

It is clear from Figure 7 that the lugworm's energy cost of breathing, $\dot{M}_{O_2}^{CB}$, evaluated as $1g\dot{M}_{O_2}^{TOT}$ *minus* $\dot{M}_{O_2}^{CONF}$, varies considerably and is generally high, the $\dot{M}_{O_2}^{CB}$ *vs* $1g\dot{M}_{O_2}^{TOT}$ ratio varying between 0.14 and 0.64, with a mean value at 0.47. Our previous, more qualitative evaluations (Toulmond, 1975; Toulmond and Tchernigovtzeff, 1984; Toulmond, 1986) are directly confirmed, and it is demonstrated that the lugworm's ventilatory piston pump is energetically expensive.

$\dot{M}_{O_2}^{CB}$ has rarely been directly evaluated in invertebrates. The most recent studies on the energetics of invertebrate water pumps give the following values of the $\dot{M}_{O_2}^{CB}$ *vs* $\dot{M}_{O_2}^{TOT}$ ratio: 0.02 in the ascidian *Styela clava* (data from Riisgård, 1988); 0.03 in the polychaete *Sabella penicillus* (Riisgård and Ivarsson, 1990); 0.09 in the bivalve *Mytilus edulis* (data from Jørgensen *et al.*, 1988); 0.2 in *Chaetopterus variopedatus,* another polychaete (data from Riisgård, 1989); and 0.30 to 0.48 in *Urechis caupo* (Pritchard and White, 1981). The first three species have ciliary pumps. *Chaetopterus* and *Urechis,* like the lugworm, have a muscular piston pump and exhibit the highest $\dot{M}_{O_2}^{CB}$ *vs* $\dot{M}_{O_2}^{TOT}$ ratios. It is clear that a piston pump consumes a sizable amount of the total quantity of oxygen it obtains from the environment.

The flow rates we measured were never very high, between 0.02 and 0.12 ml/s in *Arenicola* #21 (Fig. 2). This compares well with data recalculated from values measured by previous authors in normoxic lugworms of various sizes: 0.02 to 0.12 ml/s (Van Dam, 1938); 0.03 to 0.07 ml/s (Krüger, 1964); 0.01 to 0.03 ml/s (Jacobsen, 1967); 0.01 to 0.02 ml/s (Foster-Smith, 1978). In *Arenicola* #21, the corresponding mean value of the specific ventilation, $\dot{V}w/sh\dot{M}_{O_2}^{TOT} = 5$ l/mmol O_2, which is practically identical to that measured in normoxic lugworms (Toulmond and Tchernigovtzeff, 1984), is exceedingly low compared to values (in liters per millimole of O_2) reported for filter feeders: 7930 in *Sabella penicillus* (Riisgård and Ivarsson, 1990); 900 in the occasional suspension feeder *Nereis diversicolor* (Riisgård, 1991); and 560 to 1120 in *Chaetopterus variopedatus* (Riisgård, 1989). Jørgensen *et al.* (1986b) consider that filter feeders inhabiting coastal

waters typically process 340 l or more of water for each millimole of O_2 consumed. When considering the extremes of this set of specific ventilation values, it is easy to calculate that the O_2-extraction coefficient is about 80 to 1600 times lower in filter feeders (Ew_{O_2} between 0.0005 and 0.01) than it is in the normoxic lugworm (Ew_{O_2} = 0.82 ± 0.05, N = 37, in *Arenicola* #21). The filter feeders, which process very large volumes of water to get enough food, are practically in equilibrium with the ambient medium as far as oxygen is concerned, and their oxygen needs are easily satisfied (Hazelhoff, 1939; Jørgensen, 1955), even when ambient hypoxia is severe (Massabuau *et al.*, 1991).

Foster-Smith (1978) postulated that the pumping mechanism of an animal must have been selected to work considerably below its maximum power most of the time. If the hypothesis is correct, then a relatively large change in the resistance of the system must have only small effects on the pumping rate. Our results effectively show that changing the resistance in our experimental setting makes little difference to pumping rate (Fig. 2) and to cost of breathing (Fig. 7). In the lugworm, the piston pump operates at rather high values of ΔPHYD, up to 430 Pa in *Arenicola* #21 (Fig. 3). This value agrees roughly with previous records in the literature (Foster-Smith, 1978; Toulmond *et al.*, 1984) and is well below the maximal possibilities of a lugworm. Actually, ΔPHYD values between 1000 and 1500 Pa were commonly observed in our experimental setting. Thus the hydrostatic pressure that can be developed by the piston pump of *Arenicola* is much higher than those that have been measured in filter feeders. Jørgensen *et al.* (1986a) give an upper limit of 50 Pa to the maximum pressure that can be developed by the bivalve ciliary pump. Even in those filter feeders that have a ventilatory piston pump, the maximal operating pressures are much lower than in the lugworm: about 80 Pa in *Chaetopterus* (Riisgård, 1989) and *Nereis diversicolor* (Riisgård, 1991); less than 100 Pa in *Urechis caupo* (Chapman, 1968). Obviously, in natural conditions, the lugworm needs a more powerful engine to overcome the resistance created by the sediment that blocks the blind head-end of its gallery. The mean values of our artificial resistances R1 and R2, calculated as the slopes of the regression lines in the ΔPHYD *vs* V̇w graph of Figure 5, were respectively about 2600 and 5900 Pa·s/ml. From the values of ΔPHYD and V̇w that can be found or calculated from data in the literature, the resistance R = ΔPHYD/V̇w against which a given biological pump has to work to process water for filtration or respiratory purposes, or both, can be estimated. The values we found were (in Pa·s/ml) about 750 in *Urechis* (Chapman, 1968); 50 in *Chaetopterus* (Riisgård, 1989) and *Nereis* (Riisgård, 1991); 20 to 10 in *Mytilus* (Jørgensen *et al.*, 1986a); 10 in *Styela* (Riisgård, 1988); and 0.1 in *Sabella* (Riisgård

and Ivarsson, 1990). These resistances are much lower than those we used in our experimental setting. Do such high resistances occur in natural conditions? There are no direct data. R1 and R2 were in fact chosen to avoid the worms' turning around head to tail in the glass tube; this behavior is common when the system resistance is too high and is also observed in *Chaetopterus* (Riisgård, 1989). The fact that our animals continued to pump against R1 and R2 means that these resistances must approximate those against which the lugworms have to work in natural conditions.

Figure 4 shows that the mechanical power developed by the piston pump of *Arenicola* #21 during normal ventilation, and calculated as $\dot{W}_{MEC}$ = ΔPHYD × V̇w, is very low compared to the energy cost of breathing, $\dot{M}_{O_2}^{CB}$. The efficiency of the pump, calculated as the ratio $\dot{W}_{MEC}/\dot{M}_{O_2}^{CB}$, is low or very low, depending on which run is considered, with a mean value of about 1% as in other tested animals. However, this efficiency is certainly underestimated, since $\dot{W}_{MEC}$ is only one part of the total mechanical power, $\dot{W}$, that is actually developed by the ventilating lugworm, and corresponds only to the work done on the water expelled from the experimental gallery. We know nothing about the work done inside the animal body: to each stroke volume of water ventilated in the headward direction must correspond an identical volume of coelomic fluid and blood moving backward inside the animal. We also do not know how much work is done by the body wall muscles forming and maintaining the peristaltic wave that acts as the piston of the pump. As far as we know, these two mechanical works have never been examined experimentally. We also did not take into account the mechanical work done to fill the posterior compartment of the apparatus, but this can be considered negligible owing to the very wide opening and very low resistance of the inlet tubing (Fig. 1). However, even if we consider that the sum of these three types of unmeasured mechanical work is approximately equivalent to the work necessary to expel water from the gallery, the pump efficiency is still only two times higher than previously estimated and remains very low, at about 2%.

Conclusion

To conclude, it is clear that in *Arenicola,* which ventilates its gallery with a piston pump, the cost of breathing is very high. However, it appears from the above discussion that we cannot precisely calculate the real mechanical efficiency of the process of breathing in the lugworm. This kind of difficulty has been met by Scheid (1987), in a comparison of the costs of breathing in mammals and fishes, and originates in the fact that, whatever animal is considered, breathing is a complex activity that cannot be completely isolated from some other functions such

as, in the case of the lugworm, the circulation of the blood and of the coelomic fluid.

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Appendix

List of symbols

$M_{O_2}^{TOT}$, $\dot{M}_{O_2}^{TOT}$:	Total oxygen uptake, μJ, and total oxygen uptake rate, μW.
$sh\dot{M}_{O_2}^{TOT}$:	"Short duration" total oxygen uptake rate, μW.
$lg\dot{M}_{O_2}^{TOT}$:	"Long duration" total oxygen uptake rate, μW.
$M_{O_2}^{CONF}$, $\dot{M}_{O_2}^{CONF}$:	Basal metabolic oxygen uptake, μJ, and basal metabolic uptake rate, μW, obtained using the confinement method.
$M_{O_2}^{CB}$, $\dot{M}_{O_2}^{CB}$:	Energy cost of breathing, μJ, and rate of energy cost of breathing, μW.
$\Delta M_{O_2}^{STO}$, $\Delta \dot{M}_{O_2}^{STO}$:	Change in the oxygen stores, μJ, and rate of change in the oxygen stores, μW.
$\dot{W}_{MEC}$:	Mechanical power, μW.
PI_{O_2}, PE_{O_2}:	Oxygen partial pressure in inspired (I) and expired (E) water, kPa.
CI_{O_2}, CE_{O_2}:	Oxygen concentration in inspired (I) and expired (E) water, mmol/ml.
Vw, $\dot{V}w$:	Ventilatory flow, ml, and ventilatory flow rate, ml/s.
$\Delta PHYD$:	Hydrostatic pressure difference, Pa.
R1, R2:	Two different hydraulic resistances, $Pa \cdot s/ml$.